Beaver Dam Influence on Fish Distribution
in Lentic and Lotic Habitats
in the Black River Drainage, Alaska

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Abstract

During summer 2000, fish distribution patterns were examined in three oxbow lakes with beaver dams across outlet streams, as well as in the adjacent river in interior Alaska. Sampling was conducted with 5 cm and 11 cm stretched mesh gillnets on three occasions; mid-June, late July, and mid-September. All fish captured were measured, weighed, and sexed. Feeding condition was noted for all fish and stomach contents of feeding fish were identified when possible. Otoliths were collected for age estimation. Electronic stream gauges recorded the time and duration of high flow events that allowed fish passage over beaver dams. A total of six fish species were captured during the project. Northern pike, humpback whitefish, least cisco, and broad whitefish made up more than 98% of the catch. A single inconnu, a single Arctic grayling, and two individuals of a hybrid whitefish form were also captured. Two additional species, longnose sucker and Arctic lamprey, were identified in northern pike stomachs. Adults of the four primary species were captured in lentic (lake) and lotic (flowing water) habitats. Juveniles were captured in lentic habitat only. Relative fish abundance, based on catch-per-unit-effort, was different among study lakes, and was greater in lentic than lotic habitat. High flows in the drainage provided multiple opportunities for fish to move over beaver dams during the season. These results suggest that fish actively exploit lentic habitat despite periodic restrictions to their movements caused by beaver dams and low flows.

Table of Contents

List of Figures

List of Tables

Introduction

Eighteen fish species have been documented in the Yukon Flats region of Alaska, including three species of Pacific salmon *Oncorhynchus* spp., six coregonid species (subfamily: coregoninae; commonly referred to as whitefish), northern pike *Esox lucius*, Arctic grayling *Thymallus arcticus*, longnose sucker *Catostomus catostomus*, and others (USFWS 1990). Some fish, such as the Pacific salmon species, are known to be highly migratory, spending only a small part of their lives in the region, while others, such as northern pike and Arctic grayling, are thought to remain there throughout life. Despite our understanding of fish presence in the area, and the general life histories of certain species, our knowledge of their specific habitat needs through a season, a year, or a lifetime is minimal.

Beaver dams across waterways alter flow patterns, create lentic (lake) habitats, and influence fish distribution (Naiman et al. 1988). Dams impound water that would otherwise flow away. Surface area increases and water becomes warmer (McRae and Edwards 1994). Aquatic plant and invertebrate communities shift from lotic (flowing water) to lentic forms (McCafferty and Provonsha 1983; McDowell and Naiman 1986). Thus, beaver dams in river drainages increase habitat heterogeneity by producing patches of lentic habitat amidst a more extensive lotic environment (Naiman et al. 1988). Fish exploit these areas and segregate by species and age classes among habitats (Murphy et al. 1989; Schlosser 1995). This tendency of fish to sort by habitat led Snodgrass and Meffe (1999) to characterize many species observed in their study as either "pond fish" or "stream fish" accordingly.

While impoundments created or maintained by beaver dams provide habitat heterogeneity to an aquatic ecosystem, they also impede free movement of fish during periods of low flow (Keast and Fox 1990; Schlosser 1995). From an ecological perspective, habitat heterogeneity is good (Snodgrass 1997). More ecological niches are available and species diversity increases (Krebs 1985; Smith 1992). Murphy et al. (1989), for example, found that juvenile coho salmon *O. kisutch* were much more abundant in beaver ponds than elsewhere in the Taku River watershed

in Alaska, suggesting that the habitat facilitated rearing. Schlosser (1995) and Snodgrass and Meffe (1999) similarly reported a greater abundance of juvenile fish in beaver ponds than in nearby lotic habitats in their study areas. But, restricting fish movement is often perceived to be bad. Pacific salmon fishers commonly complain about beaver dams preventing fish from reaching spawning grounds. Also, in northern regions subject to extended periods of cold weather, low dissolved oxygen levels in ice-covered ponds can cause fish mortality. Both Fox and Keast (1990) in Ontario, and Hall and Ehlinger (1989) in Michigan, document the winterkill of fish from isolated ponds. In both studies, however, larger fish perished due to low dissolved oxygen levels, while small fish survived. Thus, beaver dams clearly increase habitat heterogeneity in wetland systems, and may affect area fish in both positive and negative ways.

Beaver dams are usually limited to small streams or backwater sloughs and are routinely washed away or submerged during high flow events (Naiman et al. 1988). Dams can impede fish passage during low flow periods of each year. However, annual periods of high flow occur in virtually all wetland areas. Interior Alaska rivers exhibit high flows each spring as the winter's accumulation of snow and ice melts, and during the summer and fall following periods of rain (Brabets et al. 2000; Trawicki 2000). Thus, high flow events allow fish to enter or exit all but the most isolated ponds each year.

This gillnet sampling study describes and compares the distribution of fish species and age classes between lentic habitats influenced by beaver dams, and nearby lotic habitats in the Black River drainage, Alaska, during summer 2000. Specific objectives were to identify fish species present, describe length, weight, and age distributions, assess feeding and spawning condition, estimate relative abundance, and compare these qualities between lentic and lotic habitats. Additionally, high flow periods were monitored to document opportunities for fish movement between habitats. The implications of our findings are discussed.

Study Area

The Black River drainage in eastern interior Alaska (Figure 1) drains the northwest flanks of the Ogilvie Mountains, a non-glaciated upland region along the Alaska-Yukon Territory border. Much of the drainage falls within the Yukon Flats National Wildlife Refuge. The region experiences a continental subarctic climate characterized by long, cold winters and brief, warm summers. Rivers and lakes generally freeze by early October and remain frozen until May. Annual precipitation in the region may total 20 cm or more (Brabets et al. 2000; Trawicki 2000).

In the upper reaches of the Black River drainage the water is clear and flows swiftly over a rocky substrate, while in the lower reaches it is stained and meanders over a soft, fine substrate. Flow rate is governed by snowmelt and rainfall, and groundwater maintains a baseflow throughout the winter months (Trawicki 2000). The lowland region of the drainage is peppered with numerous thaw lakes and oxbows, some distant from the riparian zone and isolated from the river, and others within the riparian zone and seasonally connected to the river.

Methods

Study sites

Three oxbow lakes in the lower reaches of the Black River drainage were selected for this study. All were north of the Arctic Circle. The lake positioned lowest in the drainage (L) was about 65 river km from the mouth of the Black River at approximately 66°42' N latitude, 144°16' W longitude (Figure 2). The lake positioned intermediate of the three (M) was about 115 river km from the mouth at approximately 66°43' N latitude, 143°57' W longitude (Figure 3). The lake positioned farthest upstream (U) was about 150 river km from the mouth at approximately 66°41' N latitude, 143°42' W longitude (Figure 4). The river and surrounding wetland topography appeared similar at all sites. The lakes were roughly the same size, 5-6 km long and 50-100 m wide through much of their lengths. Each had a single, narrow, stream connection to the river.

The streams ranged in length from approximately 400 m to 3 km. Beaver dams were established across all three stream connections and prevented fish passage during periods of low flow. Flow from lake drainage basins to the Black River was minimal, except during spring snowmelt or following heavy rain. During periods of high flow in the Black River, water rose above beaver dams and flooded the lakes. All three lakes had extensive shallow regions with emergent and submergent vegetation. All three had extensive regions of relatively deep water free of visible vegetation. Maximum depths were undetermined, but were greater than or equal to 4 m in some areas of each lake.
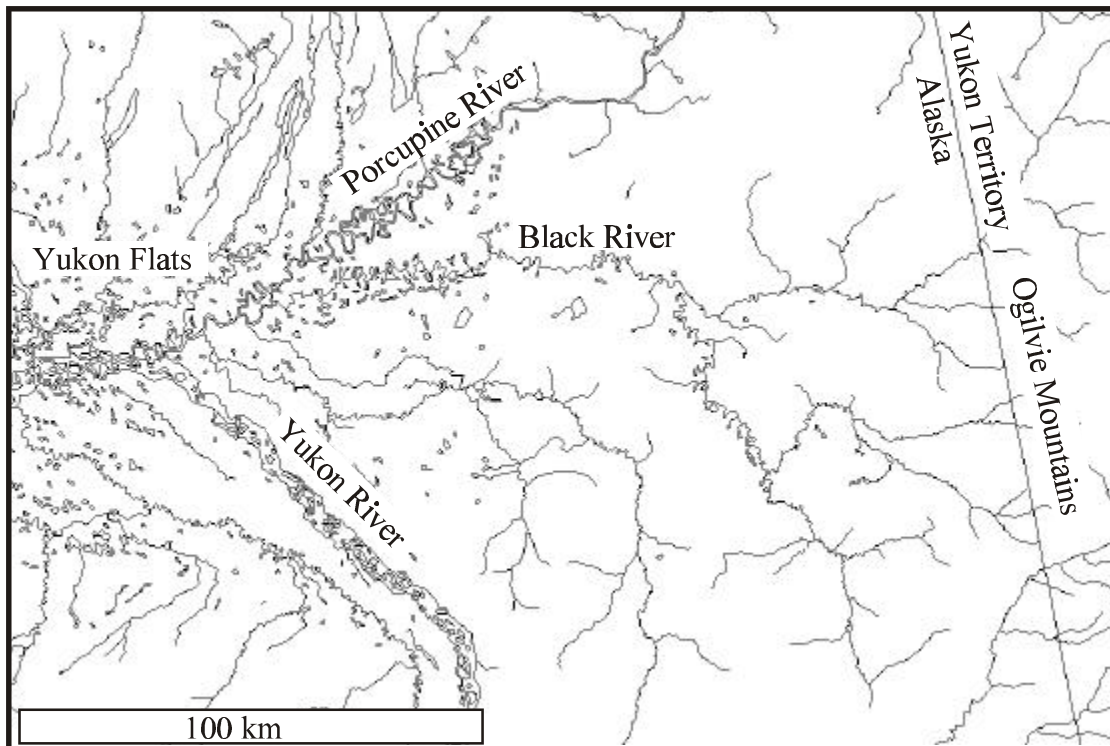
FIGURE 1.—The Black River drainage in eastern interior Alaska. Study sites for this project were located in the lower reaches of the Black River, a low relief region of meandering waterways, sloughs, and lakes.

10
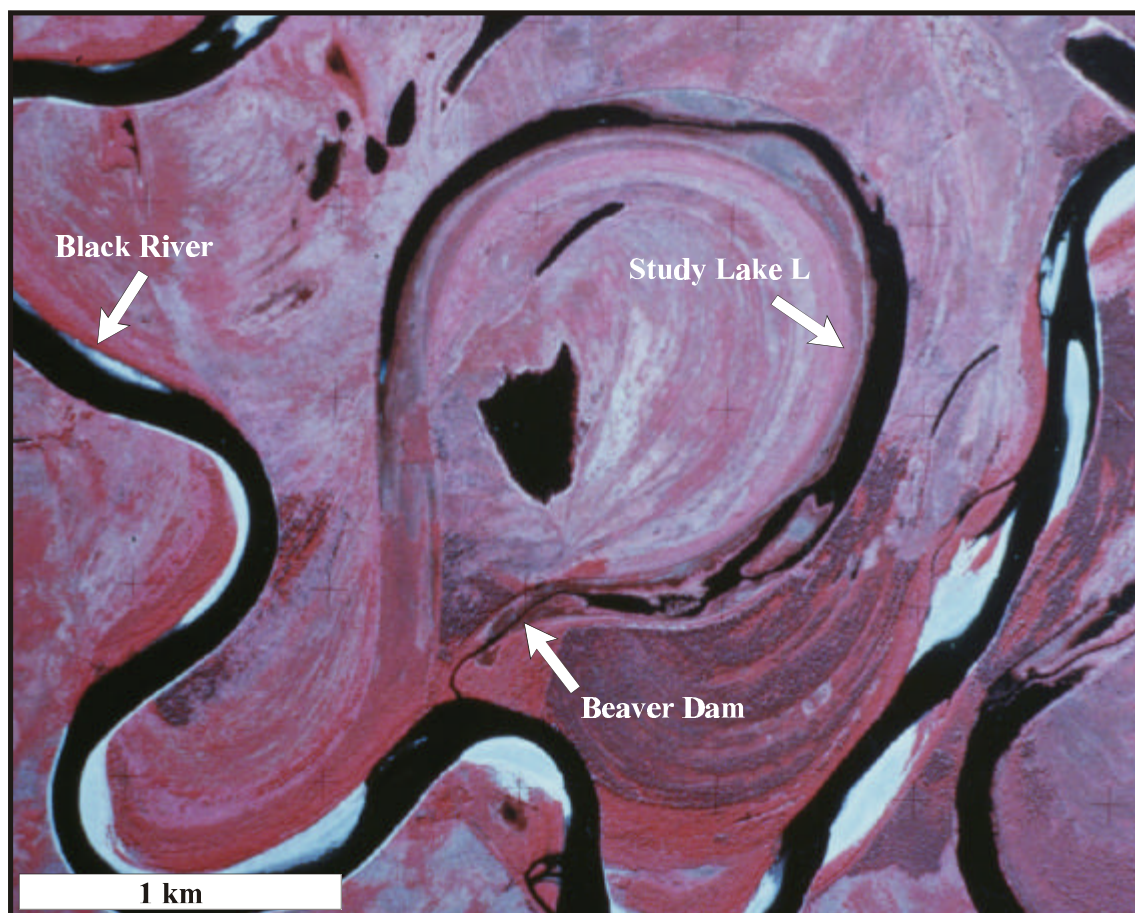
FIGURE 2.—High altitude infrared photograph of study site L, located 65 river km upstream from the mouth of the Black River.
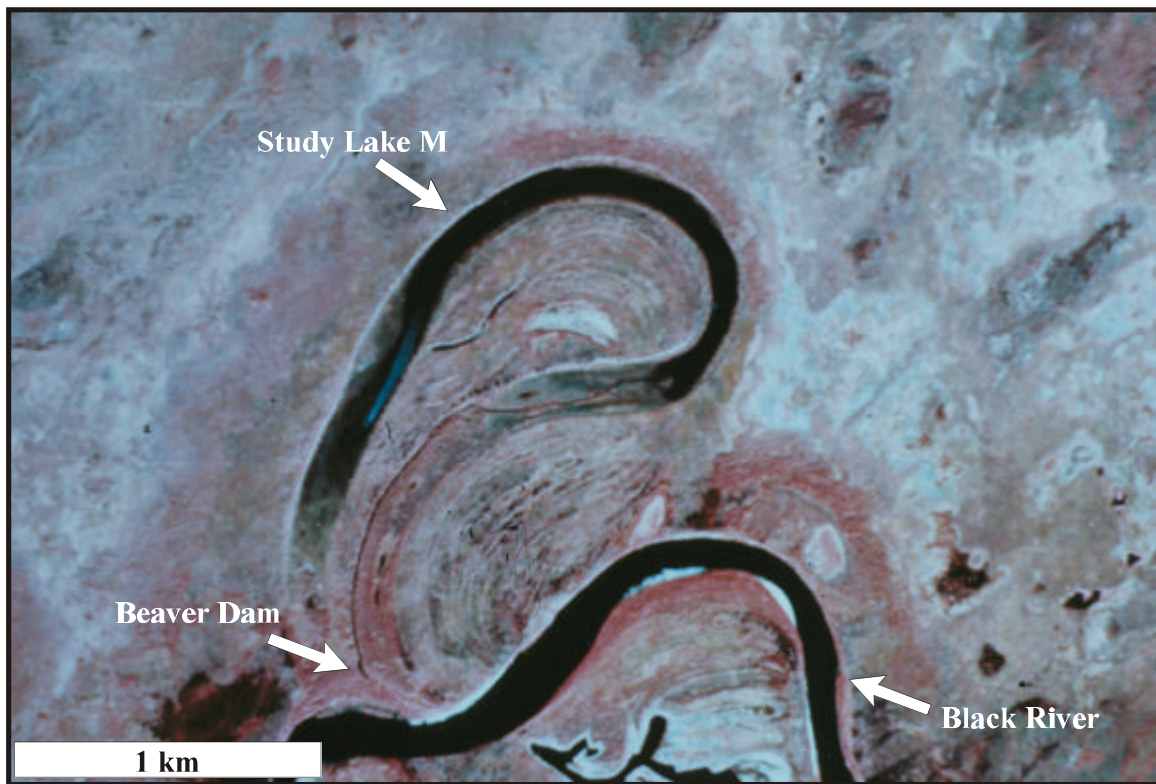
FIGURE 3.—High altitude infrared photograph of study site M, located 115 river km upstream from the mouth of the Black River.
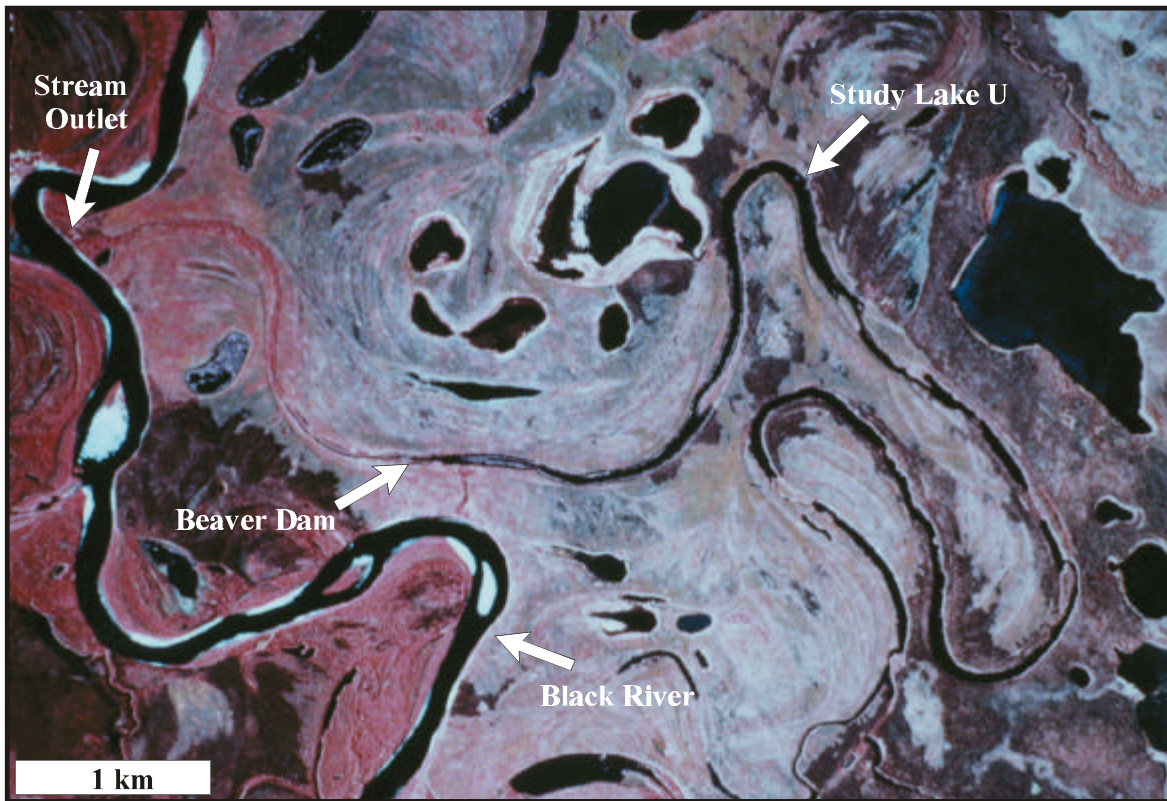
FIGURE 4.—High altitude infrared photograph of study site U, located 150 river km upstream from the mouth of the Black River.

Sampling

Systematic sampling took place in lentic and lotic habitats at all three study sites on three occasions during summer 2000. Sampling periods were mid-June, late July, and mid-September. Two 15 m monofilament gillnets of 11 cm and 5 cm stretched mesh webbing were set in each habitat during each sample period. A primary objective was to obtain a representative sample of fish present and vulnerable to sampling gear without risking sampling to depletion (Hilborn and Walters 1992), particularly during periods of isolation in lake habitats. Hence, sampling time varied from about 2-6 h/net, depending on catch rates. In lentic habitat, nets were set perpendicular to shore several hundred meters from each other. In lotic habitats, nets were set in the outlet streams near the river when possible, and along eddy lines or other slack water near the

13

outlet streams at each study site. The nets were set apart from each other either in upstream-downstream distance, or on opposite sides of the river. Water level was a factor in the selection of appropriate net sites in the river, so these sites changed from one sampling period to the next.

All fish were identified to species and subjected to a series of measurements, observations, and collection activities following capture. Fork lengths were recorded to the nearest cm. A digital platform scale was utilized to weigh each whole fish to the nearest 0.01 kg. Sex was determined based on gonad identification, although some juvenile fish were too immature to be sexed. Feeding condition, the presence or absence of food in the stomach, was noted for all captured fish. Egg skeins of female fish were removed from the body and weighed to evaluate spawning readiness (Strange 1996), and sagittal otoliths (otoliths) were collected for age estimation (Chilton and Beamish 1982).

Feeding condition and spawning readiness

Stomach contents and feeding condition data of certain species were evaluated further. Stomach contents of piscivorus species were identified to species when possible, and to family or subfamily level for others. The habitat in which the piscivorus fish was captured was noted for all fish thus identified. Once reaching maturity, coregonid fish may spawn multiple times, but rarely if ever on sequential years (Reist and Bond 1988; Lambert and Dodson 1990). As a result, mature spawners and non-spawners of a species may be present in any given sample (Reist and Bond 1988). Generally, those preparing to spawn cease feeding for a period of weeks or months prior to their fall spawning periods (Petrova 1976; Dodson et al. 1985; Prasolov 1989). Hence, feeding data for coregonid fish can be used to evaluate spawning readiness.

Spawning readiness of coregonid fish can be evaluated in other ways as well. All coregonid fish spawn in the fall (McPhail and Lindsey 1970). As spawning time approaches, egg mass increases, raising the ratio of egg to body mass (Snyder 1983). Bond and Erickson (1985) documented a rise from about 5% egg mass in July to more than 15% egg mass in late September

14

and October for several coregonid species in northern Canada. Mature non-spawning females carry eggs, but the mass remains low throughout the summer. Thus, a very clear distinction can be made regarding spawning readiness of coregonid fish. Egg skeins of female coregonid fish in this study were weighed to produce a gonadosomatic index (GSI), calculated as

$$GSI = (egg\ weight/whole\ body\ weight) \times 100,$$

to evaluate spawning readiness (Strange 1996).

Otolith preparation and fish aging

Otoliths were rinsed with water in the field and stored in paper envelopes for laboratory processing. One otolith from each fish was thin-sectioned in the transverse plane (Secor et al. 1991) using procedures detailed by Brown (2000). Prepared otoliths were viewed with a compound microscope using transmitted light and darkfield techniques. Annuli identification criteria followed basic descriptions by Chilton and Beamish (1982) and illustrations by Haas and Recksiek (1995). Charts were prepared to illustrate age-frequency distributions between habitats.

Species richness

Species richness, the number of species present (Krebs 1985), was determined for both habitats at all study sites. The similarity in species richness between habitats and study sites was evaluated with Sorensen's "coefficient of community similarity" (CC) as detailed by Smith (1992). The CC was calculated as

$$CC = (2c)/(S_1 + S_2),$$

where c = number of species common to both habitats, and S_1 and S_2 are the number of species in habitats one and two respectively (Smith 1992). The CC is a simple index that approaches one as

the proportion of shared species increases, and declines to zero as the proportion decreases. It is not a very powerful measure of similarity or difference between communities, particularly when species richness is low, but it does allow a relative assessment of community similarity between habitats.

Catch-per-unit-effort

Fish communities are described in part by identifying the species that are present, but also by each species' relative abundance within the community (Krebs 1985). In practice, relative abundance of species in a community is exceedingly difficult to estimate, and is usually done through intensive sub-sampling of a habitat, often to depletion (Hilborn and Walters 1992), a technique used by both Schlosser (1995) and Snodgrass and Meffe (1999). Alternatively, catch rates in the form of catch-per-unit-effort (CPUE) data may be used to obtain a more general understanding of abundance and rarity of species, if one assumes that CPUE is proportional to fish density (Hubert 1996). Hilborn and Walters (1992) discuss variable catchability, sampling bias, and other difficulties with this assumption when CPUE data are used to describe exploited fisheries or to create population models. None-the-less, CPUE index values in this study were assumed to be roughly proportional to fish density, at least within species, and were used to compare relative abundance of fish between lentic and lotic habitats by study site, sample period, and species. Catch-per-unit-effort was calculated as the number of fish captured per hour of net time
(fish$\cdot$h$^{-1}\cdot$net^{-1}). Net time for a particular sampling period and habitat was the sum of time from the pair of nets. Charts were prepared to illustrate patterns.

Water level monitoring

Opportunities for fish to move between lentic and lotic habitats over beaver dams were identified using remote electronic stream gauges (gauges) in the study lakes. Gauges were installed during the mid-June sampling period, and removed following the mid-September sampling period.

Water level was recorded every 30 min during this time interval. The gauges were capable of measuring maximum water level changes of 2 m, and according to the manufacturers the measurements were accurate to about 2 cm. The gauges were positioned so the lower region of the 2 m range was in the water when flow was low and beaver dams were impeding further declines in lake water level. When lake water levels rose, whether from high flow within lake drainage basins, or from the Black River flooding over the dams from outside, the gauges registered the time, duration, and magnitude of the events. A reasonable determination of times during which fish could and could not move between the lakes and the river was thus obtained. In addition, matching high flow events recorded on all three gauges allowed a rough assessment of the relative heights of the beaver dams, as the Black River affected all three.

Statistics

The proportions of fish captured in lentic versus lotic habitat were estimated for all fish combined and for each species individually. Null hypotheses, ho: proportion captured in lentic habitats = 0.5, vs ha: proportion captured in lentic habitats $\neq$ 0.5, were tested with a procedure based on the binomial probability distribution detailed by Conover (1999). Accepting the null hypothesis would imply that fish were not sorting in a significant manner between habitats. Rejecting the null hypothesis would imply that they were. Significant differences were based on " = 0.05 in all cases.

Null hypotheses that fish length, weight, and age distributions in lentic habitats were equal to those in lotic habitats were evaluated with Mann-Whitney nonparametric tests (Conover 1999). Significant differences were based on " = 0.05 in all cases.

17

Results

Capture data

Two hundred eighty-six fish of six species, as well as a hybrid form, were captured during the course of this project. Northern pike, humpback whitefish *Coregonus pidschian*, least cisco *C. sardinella*, and broad whitefish *C. nasus* made up more than 98% of the catch. A single inconnu *Stenodus leucichthys*, a single Arctic grayling, and two individuals of a hybrid coregonid form completed the tally (Table 1). In addition to fish captured directly, prey found in northern pike stomachs were examined and identified to species or subfamily level when possible. The remains of 78 fish were identified in this way. Northern pike and coregonid spp. made up almost 95% of identifiable prey items, and over 90% of these were small, roughly 5 cm fork length, and assumed to be age-0 fish. Longnose sucker and Arctic lamprey *Lampetra japonica* (a 43 cm long adult) completed the tally (Table 2). In addition to fish prey, two bald eagle chicks were discovered in the stomachs of northern pike captured during the June sample period at site L. The young birds must have fallen from a nest just prior to the sampling event.

TABLE 1.—Total fish captured by species and habitat.

Name *Species*	Abbreviation	Lentic	Lotic	Total
Northern Pike *Esox lucius*	NP	108	52	160
Humpback Whitefish *Coregonus pidschian*	HBWF	42	20	62
Least Cisco *Coregonus sardinella*	LC	32	1	33
Broad Whitefish *Coregonus nasus*	BWF	21	6	27
Inconnu *Stenodus leucichthys*	IN	1	0	1
Arctic Grayling *Thymallus arcticus*	AG	0	1	1
Hybrid Coregonid (subfamily: Coregoninae)	Hyb	2	0	2
Total		**206**	**80**	**286**

TABLE 2.—Prey of northen pike identified by species or subfamily, and by habitat of consumer.

Name *Species*	Abbreviation	Lentic	Lotic	Total
Northern Pike *Esox lucius*	NP	40	0	40
Humpback Whitefish *Coregonus pidschian*	HBWF	1	0	1
Least Cisco *Coregonus sardinella*	LC	1	3	4
Longnose Sucker *Catostomus catostomus*	LNS	3	0	3
Arctic Lamprey *Lampetra japonica*	AL	1	0	1
Unidentified Coregonid (Coregoninae spp.)	Unk	29	0	29
Total		**75**	**3**	**78**

Species richness

Species richness was low compared to typical fish communities in more southerly latitudes (Smith 1992). Six species were captured in this study (Table 1), all previously documented in the region (USFWS 1990). However, not all species were captured in all sampling periods, study sites, or habitats (Tables 3, 4, and 5). Four species were captured at study lake L, five at study lake M, and two at study lake U. Three species were captured in lotic habitat at all three study sites, although northern pike was the only species common to all three.

The CC index provided a relative measure of similarity of fish communities among study lakes and between lentic and lotic habitats. Based on the study capture record, no two sites or habitats had the same community of species, so in no case was the CC equal to one. Similarly, all sites and habitats shared at least one species in common, so the CC never declined to zero. Of particular interest to this study was whether the fish communities in the study lakes were similar to each other, and whether those communities were similar to that found in the river. While the CC index was not a powerful measure of community similarity or difference in this study, primarily because of low species richness overall, it did suggest that the fish community in the lake at study site U was different than those at study sites L and M (Table 6). Additionally, the

index suggests that

the fish community in the river at study site U was substantially different than that in the lake at study site U (Table 6).

TABLE 3.—Capture record for study site L by sample period, habitat, and species.

Species	June Lentic	June Lotic	July Lentic	July Lotic	September Lentic	September Lotic	Total Lentic	Total Lotic
NP	6	7	2	3	3	5	11	15
HBWF	16	13					16	13
LC			1				1	
BWF	6	3		1	1	1	7	5
IN								
AG								
Hyb								
Total	**28**	**23**	**3**	**4**	**4**	**6**	**35**	**33**

TABLE 4.—Capture record for study site M by sample period, habitat, and species.

Species	June Lentic	June Lotic	July Lentic	July Lotic	September Lentic	September Lotic	Total Lentic	Total Lotic
NP	5	14	62	3	20	4	87	21
HBWF	20	7			6		26	7
LC		1			8		8	1
BWF	11				3		14	
IN	1						1	
AG								
Hyb								

Total	**37**	**22**	**62**	**3**	**37**	**4**	**136**	**29**

TABLE 5.—Capture record for study site U by sample period, habitat, and species.

	June		July		September		Total	
Species	Lentic	Lotic	Lentic	Lotic	Lentic	Lotic	Lentic	Lotic
NP		11	1	3	9	2	10	16
HBWF								
LC			6		17		23	
BWF		1						1
IN								
AG						1		1
Hyb					2		2	
Total	**0**	**12**	**7**	**3**	**28**	**3**	**35**	**18**

TABLE 6.—The coefficient of community similarity (CC) between selected sampling sites. Site 1 and site 2 in each row are compared. Values in S_1 and S_2 are the number of species captured at sites 1 and 2 respectively. The value in c represents the number of species common to both sample sites. Coefficient of community values approach one as the proportion of shared species increases, and declines to zero as the proportion decreases.

Site 1	S_1	Site 2	S_2	c	$2(c)/(S_1 + S_2)$	CC
Lake L	4	Lake M	5	4	$2(4)/(4 + 5)$	0.889
Lake L	4	Lake U	2	2	$2(2)/(4 + 2)$	0.667
Lake M	5	Lake U	2	2	$2(2)/(5 + 2)$	0.571
River L	3	River M	3	2	$2(2)/(3 + 3)$	0.667
River L	3	River U	3	2	$2(2)/(3 + 3)$	0.667
River M	3	River U	3	1	$2(1)/(3 + 3)$	0.333

Lake L	4	River L	3	3	2(3)/(4 + 3)	0.857
Lake M	5	River M	3	3	2(3)/(5 + 3)	0.750
Lake U	2	River U	3	1	2(1)/(2 + 3)	0.400

Catch-per-unit-effort

Capture rates, expressed as CPUE in units of fish$\cdot$h$^{-1}\cdot$net^{-1}, were greater in lentic than lotic habitats at every study site, during each sample period, and for all four primary species of fish. Considering all species and sampling periods combined, CPUE was greater in lentic than lotic habitats at all three study sites (Figure 5). Additionally, the CPUE in study lake M (4.96) was more than 2.5 times greater than in any other sampling site (Figure 5). Considering all species and study sites combined, CPUE was more than twice as great in lentic than lotic habitats during all sample periods, and was over seven times greater in lentic than lotic habitats in the July sample period (Figure 6). Considering all sample sites and sample periods combined, CPUE was more than twice as great in lentic than lotic habitats for all four primary species, and was most dramatic for least cisco, where the CPUE in lentic habitat (0.467) was more than 35 times as great as that in lotic habitat (0.013; Figure 7). And finally, when all species, study sites, and sample periods were combined, CPUE was almost three times greater in lentic (2.99) than lotic (1.04) habitats. Thus, if CPUE was proportional to fish density during the course of this study, than fish density was greater in lentic habitats than in lotic habitats.

The proportions of northern pike, humpback whitefish, least cisco, and broad whitefish caught in lentic habitat during the course of the project ranged from 0.67 to 0.97 (Figure 8). Null hypotheses, ho: the proportion of fish captured in lentic habitat = 0.5, were rejected for all four species ($P < 0.01$ in all cases). These data strongly suggest that these species are sorting themselves into lentic habitat preferentially.

Water level monitoring

Fish movement between lentic and lotic habitats at the three study sites required water levels greater than the heights of the respective beaver dams. Two possibilities existed; either high flows cresting a dam from within a lake drainage basin, or high flows in the Black River backing up over a dam and flooding a lake from below. During the June sampling period, fish could freely move

FIGURE 5.—Catch-per-unit-effort by study site for lentic and lotic habitats.
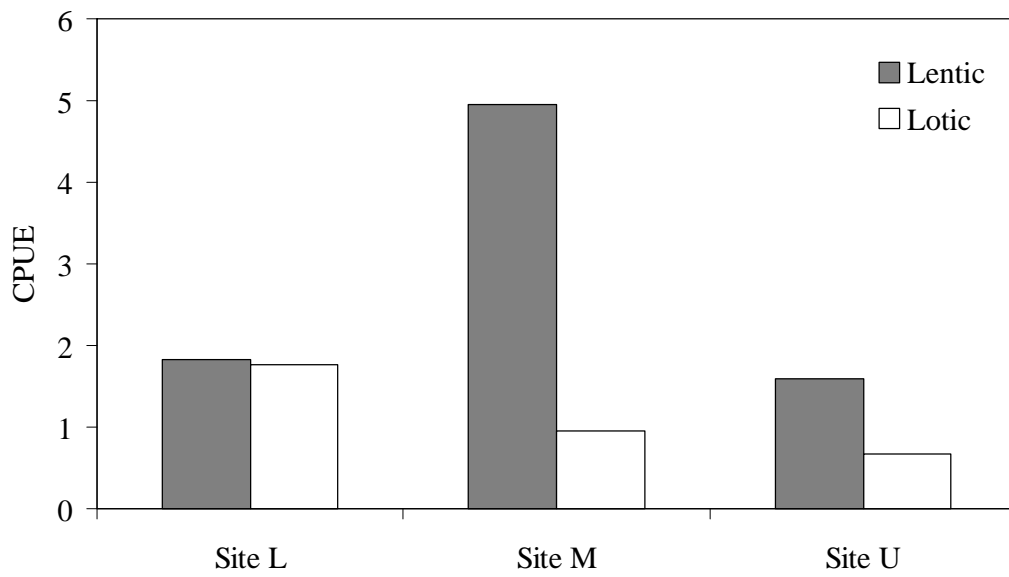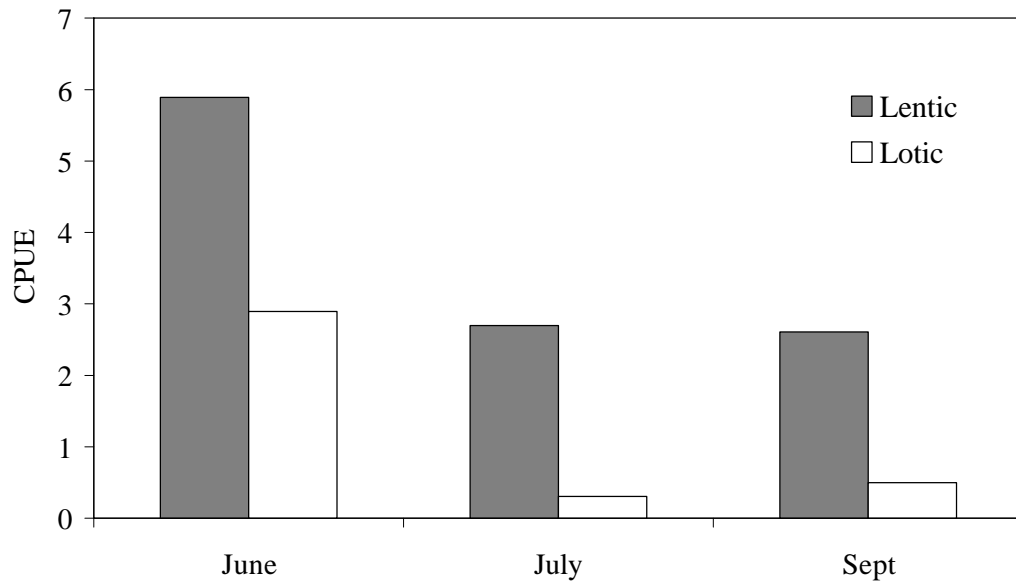

FIGURE 6.—Catch-per-unit-effort by sample period for lentic and lotic habitats.
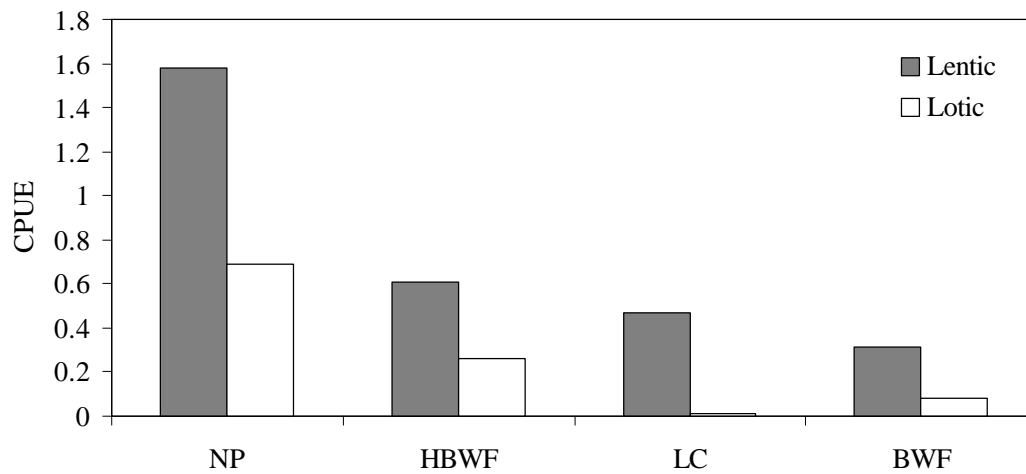
FIGURE 7.—Catch-per-unit-effort by fish species for lentic and lotic habitats.
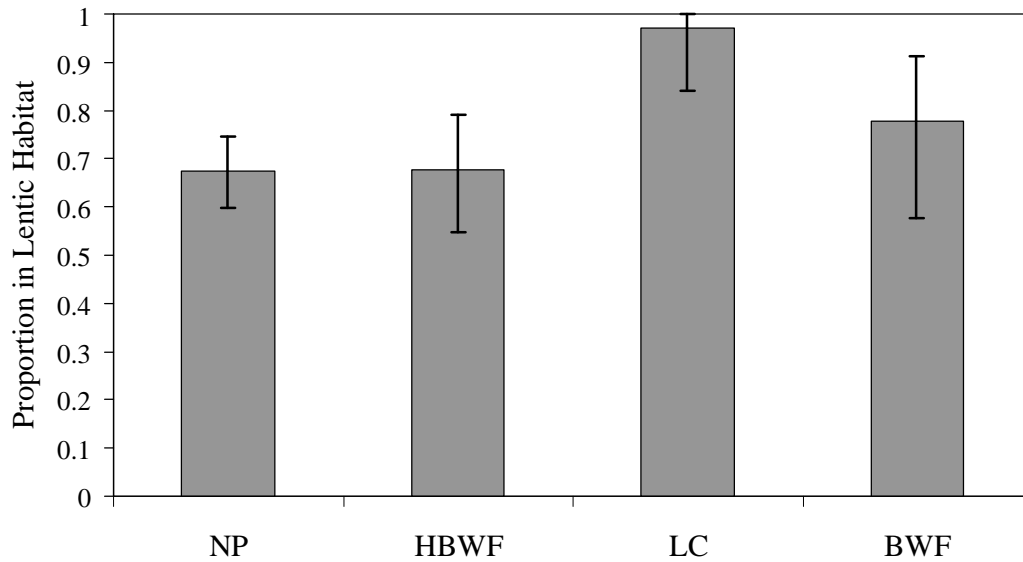

FIGURE 8.—For all four primary fish species, the proportion of total catch from lentic habitats was significantly greater than 0.5 ($P < 0.01$ in all cases). Error bars reflect the 95% confidence intervals of the estimates.

between habitats at all three sites, although at sites L and M high flows from the Black River had risen over the dams from below, while at site U, high flows from within were cresting the dam and the river water level remained below dam height. Thus, it was clear that the beaver dam at site U was higher relative to river water level than the dams at sites L and M. During the July sampling period, low flows prevented fish movement between habitats at all three study sites. At that time the beaver dam at study site L was measured at approximately 20 cm higher than river water level, while at site M, the dam was about 100 cm higher than river water level. Therefore, from on-site observations it was clear that the beaver dam at site L was lowest, site M was intermediate, and site U was highest relative to river water level.

Water level data from electronic monitoring devices indicated that fish had opportunities to move between lentic and lotic habitats at all three study sites during the course of the summer. However, variability in dam heights resulted in different frequency and duration of movement opportunities among sites. Water level was monitored for 95 days in the lake at site L, and fish had the opportunity to move between habitats 5 times for a total of 56 days, or 59% of the time period (Table 7). Water level was monitored for 95 days in the lake at site M, and fish had the opportunity to move between habitats 3 times for a total of 13 days, or 14% of the time period (Table 7). Water level was monitored for 90 days in the lake at site U, and fish had the opportunity to move between habitats 2 times for a total of 20 days, or 22% of the time period (Table 7).

High flow in the Black River in mid-August was recorded by water level monitoring devices in all three study lakes. Cross-referencing the timing and magnitudes of peak flows allowed an assessment of relative dam heights for the three lakes. Giving the dam at site L an arbitrary base height of 0 cm, the dam at site M would be 79 cm high, and the dam at site U would be 179 cm high (Table 7).

TABLE 7.—Results from the water level monitoring devices at the three study lakes, revealing the time interval of recordings, the total duration of high water events that allowed free movement of fish over beaver dams (days open), the percent of time during which free movement was possible, the number of events in which fish had free passage over beaver dams, and the relative heights of the three dams.

	Study Lake L	Study Lake M	Study Lake U
Start Day	June 11	June 9	June 15
Stop Day	September 14	September 12	September 13
Total Days	95	95	90
Days Open	56	13	20*
Percent Open	59	14	22
Open Events	5	3	2
Relative Dam Heights	0 cm	79 cm	179 cm

*It should be noted that 13 of the 20 open days were due to high flows from within the lake flowing over the dam, and only 7 of 20 open days were associated with flooding from the river.

Species accounts

Following are accounts of the four primary fish species captured during the course of this project. Length, weight, and age distributions between habitats were compared, and seasonal differences were discussed. Spawning readiness of coregonid species was evaluated.

Northern pike

Northern pike were captured at all study sites and in all habitats. However, size and age distribution was not equal among study sites or between habitats. Combining the data from all three study sites reveals that northern pike captured in lentic habitat were significantly shorter ($P < 0.001$; Table 8), lighter ($P < 0.001$; Table 9) and younger ($P < 0.001$; Table 10) than those

captured in lotic habitat. Age-1 and age-2 northern pike were captured only in lentic habitats, where they ranged from age-1 to age-14, while in lotic habitat they ranged from age-3 to age-19 (Table 10; Figure 9).

TABLE 8.—Median fork lengths (cm) of northern pike between habitats by study site. Sample sizes are indicated in parentheses. The P-values reflect the results of Mann-Whitney tests. The null hypothesis in each case is; ho: median of lentic habitat = median of lotic habitat. Asterisks indicate significant differences.

| | Lentic | | Lotic | | |
	Median (N)	Range	Median (N)	Range	P-value
Site L	66 (11)	28-87	71 (15)	58-84	0.287
Site M	34 (87)	26-79	72 (21)	51-98	< 0.001*
Site U	37 (10)	29-41	65.5 (16)	50-72	< 0.001*
Combined	35 (108)	26-87	67.5 (52)	50-98	< 0.001*

TABLE 9.—Median weights (kg) of northern pike between habitats by study site. Sample sizes are indicated in parentheses. The P-values reflect the results of Mann-Whitney tests. The null hypothesis in each case is; ho: median of lentic habitat = median of lotic habitat. Asterisks indicate significant differences.

| | Lentic | | Lotic | | |
	Median (N)	Range	Median (N)	Range	P-value
Site L	1.94 (11)	0.17-4.56	2.38 (15)	1.37-3.92	0.406
Site M	0.34 (87)	0.14-3.28	2.60 (21)	1.10-6.55	< 0.001*
Site U	0.40 (10)	0.21-0.62	1.92 (16)	0.79-2.55	< 0.001*
Combined	0.37 (108)	0.14-4.56	2.14 (52)	0.79-6.55	< 0.001*

TABLE 10.—Median ages (years) of northern pike between habitats by study site. Sample sizes are indicated in parentheses. The P-values reflect the results of Mann-Whitney tests. The null hypothesis in each case is; ho: median of lentic habitat = median of lotic habitat. Asterisks indicate significant differences.

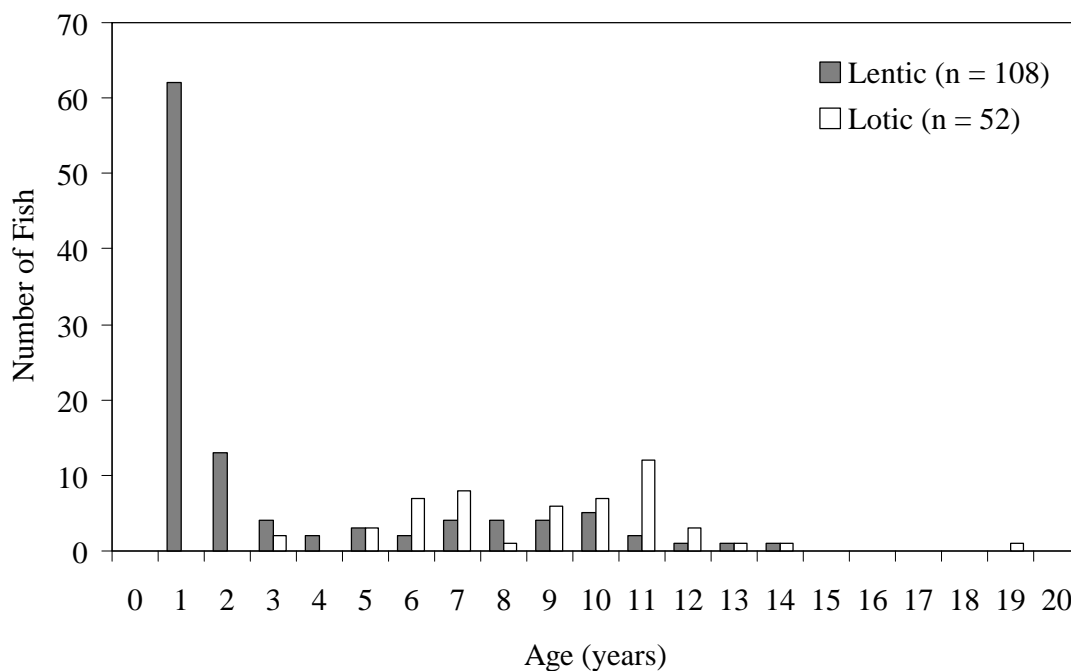| | Lentic | | Lotic | | |
	Median (N)	Range	Median (N)	Range	P-value
Site L	9 (11)	1-13	9 (15)	6-14	0.793
Site M	1 (87)	1-14	10 (21)	3-19	< 0.001*
Site U	2 (10)	1-3	6 (16)	3-11	< 0.001*
Combined	1 (108)	1-14	9 (52)	3-19	< 0.001*

FIGURE 9.—Age frequency chart illustrating the distribution of northern pike age classes between lentic and lotic habitats. Data from all study sites and sample periods are combined.

Humpback whitefish

Humpback whitefish were captured at study sites L and M in both lentic and lotic habitats, but were never captured at site U. Humpback whitefish captured in lentic habitats were not significantly longer (Table 11), heavier (Table 12), or older (Table 13) than those captured in lotic habitats. However, six age-1 immature fish were captured in lentic habitat at site M, while only mature fish were captured in lotic habitat, the youngest being age-8 (Table 13; Figure 10). Age classes between age-2 and age-7 were missing from the sample, even though they would have been vulnerable to the nets had they been present. Their absence suggests they were elsewhere.

TABLE 11.—Median fork lengths (cm) of humpback whitefish between habitats by study site. Sample sizes are indicated in parentheses. The P-values reflect the results of Mann-Whitney tests. The null hypothesis in each case is; ho: median of lentic habitat = median of lotic habitat. Asterisks indicate significant differences.

| | Lentic | | Lotic | | |
	Median (N)	Range	Median (N)	Range	P-value
Site L	45.5 (16)	42-52	47 (13)	41-51	0.259
Site M	47 (26)	21-51	49 (7)	42-52	0.250
Combined	46 (42)	21-52	47 (20)	41-52	0.196

Spawning readiness for mature humpback whitefish could not be determined with certainty. All mature humpback whitefish were captured in the June sample period. They were all feeding, which could be expected early in the season for both spawners and non-spawners. The GSI values for 25 female humpback whitefish were normally distributed around a mean value of 1.98, and ranged from 0.7 to 3.4. Both spawners and non-spawners could potentially show these relatively low values early in the season.

TABLE 12.—Median weights (kg) of humpback whitefish between habitats by study site. Sample sizes are indicated in parentheses. The P-values reflect the results of Mann-Whitney tests. The null hypothesis in each case is; ho: median of lentic habitat = median of lotic habitat. Asterisks indicate significant differences.

	Lentic		Lotic		
	Median (N)	Range	Median (N)	Range	P-value
Site L	1.26 (16)	1.07-1.58	1.33 (13)	0.95-1.71	0.148
Site M	1.28 (26)	0.11-1.72	1.49 (7)	1.01-2.03	0.086
Combined	1.27 (42)	0.11-1.72	1.42 (20)	0.95-2.03	0.054

TABLE 13.—Median ages (years) of humpback whitefish between habitats by study site. Sample sizes are indicated in parentheses. The P-values reflect the results of Mann-Whitney tests. The null hypothesis in each case is; ho: median of lentic habitat = median of lotic habitat. Asterisks indicate significant differences.

	Lentic		Lotic		
	Median (N)	Range	Median (N)	Range	P-value
Site L	15 (16)	9-30	18 (13)	8-24	0.271
Site M	11 (26)	1-24	15 (7)	8-17	0.707
Combined	12.5 (42)	1-30	15 (20)	8-24	0.143

Least cisco

Least cisco were captured at all study sites during the course of the summer, however, all but one were captured in lentic habitats, and 70% were from study site U. Neither comparisons between habitats nor among study sites were conducted, but spawning readiness was evaluated.

In the Chatanika River, Alaska, least cisco were shown to be sexually mature by age-3 (Fleming 1996). Data from this study support Fleming's (1996) findings. Visual examination of male

gonads and GSI data for female fish suggested that all least cisco age-3 and above, N = 25, were sexually mature, and those age-1 and age-2, N = 8, were immature. They ranged from age-1 to age-9, with a median of age-3 (Figure 11). Seven immature fish, four age-1 and three age-2, were captured in lentic habitat at study site M. One age-2 fish was captured in lentic habitat at study site U.
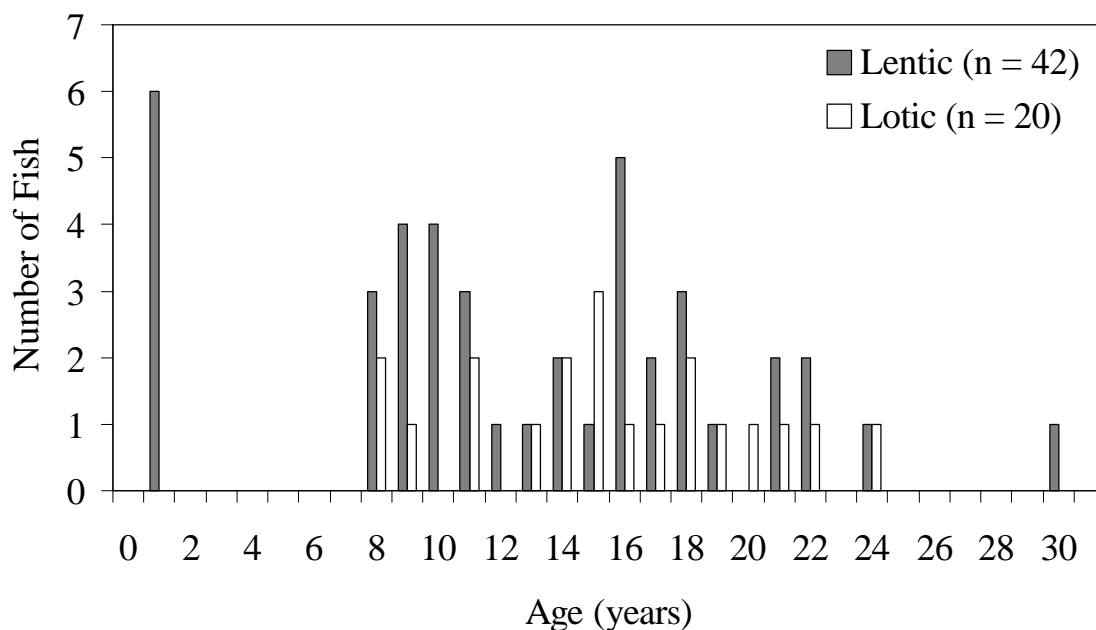

FIGURE 10.—Age frequency chart illustrating the distribution of humpback whitefish age classes between lentic and lotic habitats. Data from all study sites and sample periods are combined.

Twenty-three least cisco were captured in lentic habitat at site U (Table 5). Of these, 15 were female and 8 were male. Female and male least cisco had similar length, weight and age distributions. Gonadosomatic index values were obtained from 14 female fish, 6 captured in July, and 8 in September. Female least cisco caught in July and September had similar length, weight and age distributions. However, GSI values were significantly greater in September than in July (P = 0.002; Table 14). In addition, all least cisco were feeding in July, and only one, an

age-2 immature female, was feeding in September. The relatively high GSI values in September, along with the observation that feeding had stopped, indicate that least cisco in the lake were preparing to spawn during the fall.
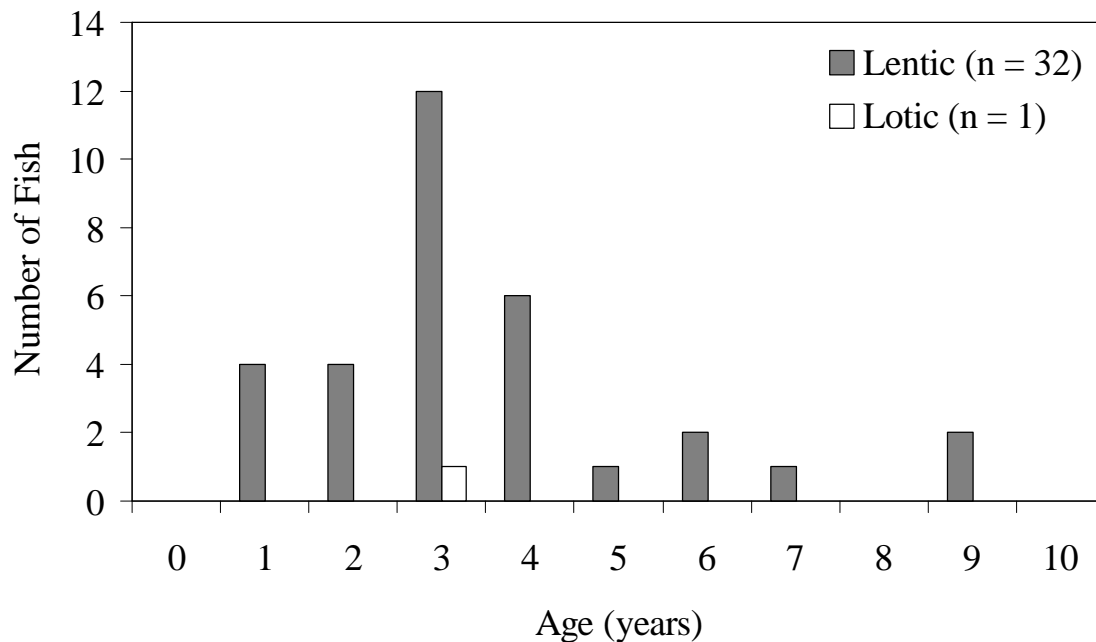

FIGURE 11.—Age frequency chart illustrating the distribution of least cisco age classes between lentic and lotic habitats. Data from all study sites and sample periods are combined.

Broad whitefish

Twenty-seven broad whitefish were captured among the three study sites (Table 1). Most were captured in lentic habitat (Figure 8), and most were captured during the June sampling period at study sites L and M (Tables 3 and 4), a time when high flows allowed fish movement between habitats. Only one was captured at study site U, and it was in lotic habitat (Table 5). Due to small sample sizes, length, weight, and age comparisons between habitats and among study sites were not conducted. None-the-less, age distribution data was prepared and spawning readiness

was evaluated.

TABLE 14.—Median fork lengths (cm), weights (kg), ages (years), and GSI values of female least cisco captured during either July or September sample periods in lentic habitat at study site U. The P-values reflect the results of Mann-Whitney tests. The null hypothesis in each case is; ho: median of July period = median of September period. Asterisks indicate significant differences.

	July (N = 6)		September (N = 8)		
	Median	Range	Median	Range	P-value
Fork length (cm)	32	30-39	34	31-36	0.558
Weight (kg)	0.51	0.42-0.95	0.55	0.41-0.64	1.000
Age (years)	4	3-9	3	3-6	0.333
GSI	4.2	2.4-6.2	16.1	14.5-17.2	0.002*

Broad whitefish ages were normally distributed around a mean value of 7.3 years and ranged from age-1 to age-14 (Figure 12). The youngest fish captured in lentic habitat was age-1, while the youngest captured in lotic habitat was age-5 (Figure 12).

Spawning readiness could be determined with certainty for only one broad whitefish. GSI values were obtained from 15 female broad whitefish, 14 captured in June and 1 in September. All 15 fish were between age-5 and age-14. Both Alt (1976) and Prasolov (1989) suggest that age-5 broad whitefish could potentially be sexually mature. GSI values from those taken in June were uniformly low, ranging from 0.5 to 4.2. Both spawners and non-spawners could have low GSI values in June. The GSI value from the fish taken in September, however, was 12, indicating that the fish was certainly preparing to spawn later in the fall.
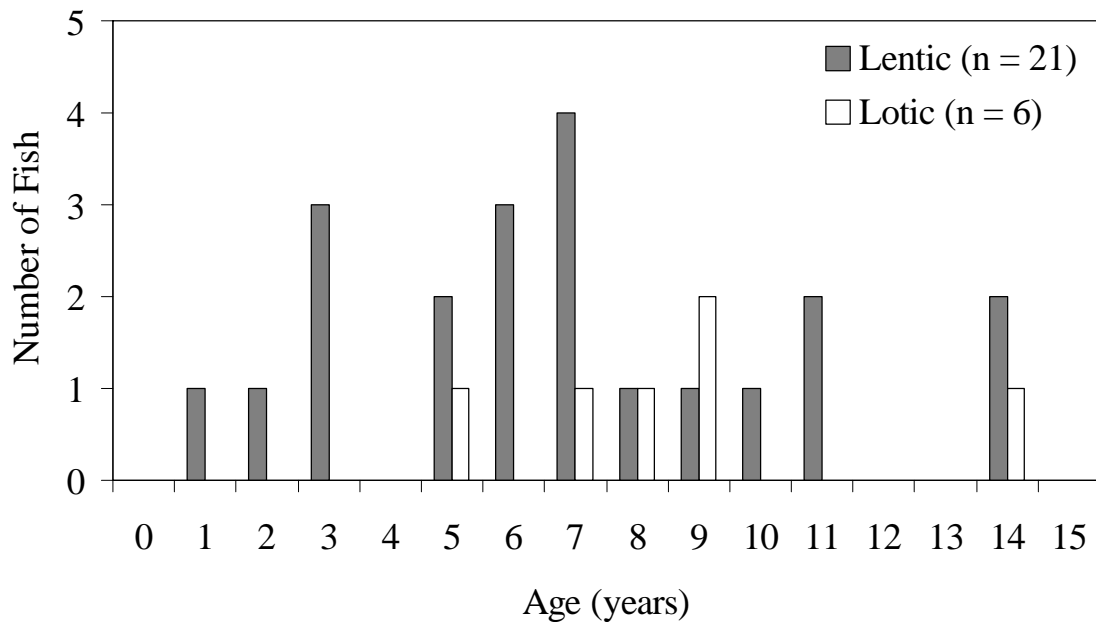
FIGURE 12.—Age frequency chart illustrating the distribution of broad whitefish age classes between lentic and lotic habitats. Data from all study sites and sample periods are combined.

Discussion

Study sites

The three lakes examined in this study were similar in geographic location, overall size, form, and proximity to the river, yet the fish communities in each were different. Fish in study lake L were similar in species present, CPUE, and age distribution to those in the river. The relatively low dam at the site permitted fish to move between habitats during more than half the summer, and the lake's water level rose and fell in conjunction with flow in the river. The largest number of fish species, the highest CPUE, and the greatest abundance of juvenile fish were found in study lake M. The intermediate height dam at the site restricted fish movement between habitats most of the summer, and water levels in the lake remained relatively stable. The fish community

in study lake U was dominated by least cisco, which were predominantly mature and preparing to spawn. Least cisco were present, but in low abundance, at the other study lakes. The relatively high dam at site U restricted fish movement through most of the summer. The lake was minimally affected by flow in the river, and its water level varied little through the summer. These results suggest that different levels of lotic influence on lentic habitat, mediated in large part by beaver dams across outlet streams, profoundly affect the composition of lentic fish communities. Naiman et al. (1986) suggest further that beaver dams confer stability to lentic habitat, and in so doing, improve the overall ecological value of the wetland system.

Juvenile fish

Juvenile fish of all four primary species were captured only in lentic habitat, primarily in study lake M. Of the 73 age-1 fish captured during the study, 62 were northern pike, 6 were humpback whitefish, 1 was a broad whitefish, and 4 were least cisco. Additionally, in the stomachs of the 62 age-1 northern pike were 70 much smaller fish that were assumed, because of their diminutive sizes, to be age-0. Forty of these small prey fish were northern pike, 27 were coregonid spp., and 3 were longnose sucker. The water level monitoring data collected during this study showed that fish had opportunities to move between lentic and lotic habitats, but capture data suggests they selected lentic habitat preferentially. Other researchers have reported similar findings. For example, Murphy et al. (1989) determined that juvenile coho salmon selected beaver pond habitat over lotic habitat for rearing in the Taku River, Alaska. Schlosser (1995) showed that juvenile fish of several species in headwater streams of Minnesota resided in beaver ponds for months, even when they had opportunities to move. And Snodgrass and Meffe (1999) reported that for many species in their North Carolina study area, juveniles were most abundant in beaver ponds, while adults were most abundant in streams. Beaver ponds on the Black River drainage appear to provide rearing habitat to juvenile fish of several species.

Hybrid coregonids

Hybrid coregonid fish have been described by Berg (1962) in the U.S.S.R., Alt (1971) in Alaska, Reist et al. (1992) in Canada, and others. Parental species of hybrid forms have been inferred by the similarity of hybrids to potential parent species in outward appearance, meristic count analyses, and genetic data. Hybridization is thought to occur because of accidental fertilization resulting from temporal and geographic proximity of spawning fish from multiple species, rather than true cross-species mating. Therefore, recognition of hybrid forms, and identification of parent species can reveal that species share spawning time and place. Recognition of hybrid coregonid forms requires a familiarity with potential parent species in the region, and the observation that a particular fish can not be classified as one of those species.

Two hybrid coregonid fish of the same form were captured in this study during the September sample period in study lake U. Both were associated with least cisco. Their general body form was most similar to least cisco, but not too unlike humpback whitefish or broad whitefish. All three were present in the Black River drainage and were considered as potential parent species. Both hybrid fish had terminal mouths, unlike either the protruding lower jaw characteristic of least cisco or the subterminal mouths of humpback whitefish and broad whitefish. Both had a subtle dorsal hump behind the head, a feature not shared by least cisco, and which is more pronounced in humpback whitefish and broad whitefish. Both had scales isolated by integument similar to humpback whitefish or broad whitefish, rather than the overlapping scales common to least cisco. One hybrid was an age-8 gravid female with a GSI of 19.6, certainly preparing to spawn. The other was an immature age-3 fish of unknown sex. All age-3 least cisco in this study appeared to be mature, but humpback whitefish and broad whitefish are never thought to be mature at age-3 (Alt 1976, 1979; Reist and Bond 1988; Prasolov 1989; Fleming 1996). The eggs were pale flesh-colored, similar to humpback whitefish or broad whitefish eggs, rather than the bright yellow or orange eggs of least cisco (Morrow 1980). Neither detailed meristic counts nor genetic analyses were conducted with these fish, but their distinct outward characteristics, summarized above, revealed them as hybrid fish.

In Alaska, least cisco are known to spawn in late September or early October. In two locations where spawning has been witnessed, the Chatanika River near Fairbanks, and the Innoko River near the old mining town of Ophir, least cisco and humpback whitefish were spawning in close proximity to each other (Alt 1983; Fleming 1996). Broad whitefish spawning locations have not been identified in Alaska, but Reist and Bond (1988) in Canada, and Prasolov (1989) in Russia, both report that broad whitefish spawn from late October to late December, depending on location, too late to allow accidental spawning with least cisco. The hybrid forms captured in this study are therefore, thought to be least cisco-humpback whitefish crosses, a form reported previously by both Berg (1962) and Reist et al. (1992). The different age classes of the two hybrids suggests that least cisco and humpback whitefish may share a spawning area annually.

Conclusion

The primary objective of this study was to evaluate fish use patterns in lentic and lotic habitats in places where beaver dams periodically prevented fish movement between habitats. Water level data in the three study lakes, combined with field observations during sampling periods, showed that fish had multiple opportunities to move between habitats (Table 6). The CPUE data indicated a greater abundance of fish in lentic than lotic habitats for study sites M and U (Figure 5), during all sample periods (Figure 6), and for all four primary species captured during the study (Figure 7). Juvenile fish of all four primary species were captured only in lentic habitat (Figures 9, 10, 11, and 12), indicating that it serves as rearing habitat. Beaver dams appear to be habitat stabilizing structures that increase habitat heterogeneity in the wetland system, and by so doing, benefit fish in general, and juvenile fish specifically.

Acknowledgments

References

Alt, K. T. 1971. Occurrence of hybrids between inconnu, *Stenodus leucichthys nelma* (Pallas), and humpback whitefish, *Coregonus pidschian* (Linnaeus) in Chatanika River, Alaska. Transactions of the American Fisheries Society, 2: 362-365.

Alt, K. T. 1976. Age and growth of Alaskan broad whitefish, *Coregonus nasus*. Transactions of the American Fisheries Society, 105(4): 526-528.

Alt, K. T. 1979. Contributions to the life history of the humpback whitefish in Alaska. Transactions of the American Fisheries Society, 108: 156-160.

Alt, K. T. 1983. Inventory and cataloging of sport fish and sport fish waters of western Alaska. Alaska Department of Fish and Game, Project F-9-15, Study G-1, Volume 24: 34-71, Juneau.

Berg, L. S. 1962. Freshwater fishes of the U.S.S.R. and adjacent countries. Originally Published in Russian in 1948, Translated and Republished by Israel Program for Scientific Translations, Jerusalem, Israel.

Bond, W. A., and R. N. Erickson. 1985. Life history studies of anadromous coregonid fishes in two freshwater lake systems on the Tuktoyaktuk Peninsula, Northwest Territories. Canadian Technical Report of Fisheries and Aquatic Sciences, No. 1336.

Brown, R. J. 2000. Migratory patterns of Yukon River inconnu as determined with otolith microchemistry and radio telemetry. Master's Thesis. University of Alaska, Fairbanks.

Brabets, T. P., B. Wang, and R. H. Meade. 2000. Environmental and hydrologic overview of the Yukon River basin, Alaska and Canada. U. S. Geological Survey, Water-Resources Investigations Report 99-4204, Anchorage, Alaska.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Department of Fisheries and Oceans, Canadian Special Publication of Fisheries and Aquatic Sciences 60, Ottawa, Ontario.

Conover, W. J. 1999. Practical nonparametric statistics, 3d edition. John Wiley & Sons, Inc., New York.

Dodson, J. J., Y. Lambert, and L. Bernatchez. 1985. Comparative migratory and reproductive strategies of two sympatric anadromous coregonine species of James Bay. Pages 296-315 *in* M. A. Rankin, editor, Migration: mechanisms and adaptive significance. Contribution to Marine Science Supplement, 27.

Fleming, D. F. 1996. Stock assessment and life history studies of whitefish in the Chatanika River during 1994 and 1995. Alaska Department of Fish and Game, Fishery Data Series No. 96-19, Anchorage.

Fox, M. G., and A. Keast. 1990. Effects of winterkill on population structure, body size, and prey consumption patterns of pumpkinseed in isolated beaver ponds. Canadian Journal of Zoology, 68: 2489-2498.

Haas, R. E., and C. W. Recksiek. 1995. Age verification of winter flounder in Narragansett Bay. Transactions of the American Fisheries Society, 124: 103-111.

Hall, D. J., and T. J. Ehlinger. 1989. Perturbation, planktivory, and pelagic community structure: the consequence of winterkill in a small lake. Canadian Journal of Fisheries and Aquatic Science, 46: 2203-2209.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman & Hall, New York.

Hubert, W. A. 1996. Passive capture techniques. Pages 157-192 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Keast, A., and M. G. Fox. 1990. Fish community structure, spatial distribution and feeding ecology in a beaver pond. Environmental Biology of Fishes, 27: 201-214.

Krebs, C. J. 1985. Ecology, the experimental analysis of distribution and abundance, third edition. Harper Collins Publishers, Inc. New York.

Lambert, Y., and J. J. Dodson. 1990. Influence of freshwater migration on the reproductive patterns of anadromous populations of cisco (*Coregonus artedii*) and lake whitefish (*C. Clupeaformis*). Canadian Journal of Fisheries and Aquatic Science, 47: 335-345.

McCafferty, W. P., and A. V. Provonsha. 1983. Aquatic entomology. Jones and Bartlett Publishers, Boston.

McDowell, D. M., and R. J. Naiman. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (Castor canadensis). Oecologia (Berlin), 68: 481-489.

McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Bulletin 173, Fisheries Research Board of Canada, Ottawa.

McRae, G., and C. J. Edwards. 1994. Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for brook trout habitat. Transactions of the American Fisheries Society, 123: 641-656.

Morrow, J. E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage, Alaska.

Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K. V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Onchorynchus*) in the glacial Taku River, southeast Alaska. Canadian Journal of Fisheries and Aquatic Science, 46: 1677-1685.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (Castor canadensis). Ecology, 67(5): 1254-1269.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38: 753-762.

Petrova, N. A. 1976. The biology of the Inconnu, Stenodus leucichthys nelma, from the Irtysh River basin. Journal of Ichthyology, 16(1): 17-27.

Prasolov, P. P. 1989. On the biology of the broad whitefish, <u>Coregonus nasus</u>, from the lower
  Ob River basin. Journal of Ichthyology, 29(5): 47-53.

Reist, J. D., and W. A. Bond. 1988. Life history characteristics of migratory coregonids of the
  lower Mackenzie River, Northwest Territories, Canada. Finnish Fisheries Research 9:
  133-144.

Reist, J. D., J. Vuorinen, and R. A. Bodaly. 1992. Genetic and morphological identification of
  coregonid hybrid fishes from Arctic Canada. Pol. Arch. Hydrobiol., 39(3-4): 551-561.

Schlosser, I. J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams
  adjacent to beaver ponds. Ecology, 76(3): 908-925.

Secor, D. H., J. M. Dean, and E. H. Laban. 1991. Manual for otolith removal and preparation
  for microstructural examination. Electric Power Research Institute, and the Belle W.
  Baruch Institute for Marine Biology and Coastal Research, Technical Publication Number
  1991-01, Palo Alto, California.

Smith, R. L. 1992. Elements of ecology, third edition. HarperCollins Publishers Inc., New
  York.

Snyder, D. E. 1983. Fish eggs and larvae. Pages 165-197 *in* L. A. Nielsen, D. L. Johnson, and
  S. S. Lampton, editors. Fisheries techniques. American Fisheries Society, Bethisda,
  Maryland.

Snodgrass, J. W. 1997. Temporal and spacial dynamics of beaver-created patches as influenced
  by management practices in a North American landscape. Journal of Applied Ecology,
  34: 1043-1056.

Snodgrass, J. W., and G. K. Meffe. 1999. Habitat use and temporal dynamics of blackwater
  stream fishes in and adjacent to beaver ponds. Copeia, 3: 628-639.

Strange, R. J. 1996. Field examination of fishes. Pages 433-446 *in* B. R. Murphy and D. W.
  Willis, editors. Fisheries techniques, 2d edition. American Fisheries Society, Bethesda,
  Maryland.

Trawicki, J. 2000. Water resources inventory and assessment, Yukon Flats National Wildlife
  Refuge (water years 1993-1998). U. S. Fish and Wildlife Service, Water Resources
  Branch, Anchorage, Alaska.

USFWS (U. S. Fish and Wildlife Service). 1990. Yukon Flats National Wildlife Refuge, fishery

    management plan. U. S. Fish and Wildlife Service, Fairbanks Fishery Assistance Office,

    Fairbanks, Alaska.